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Compression of space in visual memory

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Abstract

Human observers had to point to the location of a briefly presented target by means of a mouse after a brief delay following target offset. It was found that observers systematically mislocalized the target closer to the center of gaze, and to visually salient markers in the visual display. A perceptual judgment task revealed that these errors in localization were independent of whether or not eye movements were made, and even of planning for them, thereby demonstrating that the effect was a perceptual phenomenon, not a sensorimotor one. Further experiments demonstrated clearly that the magnitude of the time interval between target presentation and judgment regarding its spatial location was the critical parameter. A longer time interval between the event and its report enhanced significantly the amplitude of compression, thus establishing this phenomenon as a visual memory effect. We conclude that visual memory of spatial location is distorted over time in a systematic, monotonic fashion as a result of the sustained fixation of the observer on a fixed location during and shortly after target presentation, or by the continual presence of stable, salient landmarks in the environment. © 2001 Elsevier Science Ltd. All rights reserved.

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Several studies have shown that subjects mislocalize the positions of targets during steady eye fixation (Osaka, 1977; Rauk & Luuk, 1978; Mitrani & Dimitrov, 1982; Mateeff & Gourevich, 1983), and in letter identification tasks (Townsend, 1973; Mewhart & Campbell, 1978) while gaze was maintained at a fixed location. These phenomena are reminiscent of Helmholtz's pioneering observation of a perceptual shortening of the length of a peripherally displayed line during steady eye fixation (Helmholtz, 1866; Sneider & Ehrlich, 1978). The mechanism underlying this kind of mislocalization still remains somewhat of a mystery. Broadly speaking, any such effect can arise either because of some form of visual misperception, as the result of imprecisely coded motor or pre-motor activity in the brain, or some combination of the above. Since the task involved pointing to the target, inaccuracies in the neural coding of movement magnitude, or motor control, can also account for the effect. Systematic mislocalizations in estimating the position of briefly presented targets

shown during saccadic eye movements (EMs) have been found (Matin, 1972; Honda, 1993, 1995; Cai, Pouget, Schlag-Rey & Schlag, 1997; Ross, Morrone, & Burr, 1997). Even under controlled conditions in which arm or eye movements are not allowed, eye movement plans and preparatory pre-motor activity could still lead to localization errors. Recently, investigators have discovered signals in single cells in the cortex related to movements that are planned but not executed (Seal & Commenges, 1985; Snyder, Batista, & Andersen, 1997). On the other hand, if this effect is perceptual or memory-based in nature, it is likely to endure whether or not motor activity takes place, and to persist even when pre-motor activity or motor planning is minimized. Even if misperceptions were the underlying cause of the mislocalization effect, there are several alternative explanations that fall in its purview. If the pattern of errors in target localization results from the lack of a veridical spatial memory, the pattern should not be observed during visual presentation but unfold gradually over time, or appear spontaneously after some relatively fixed time interval following stimulus offset. A purely perceptual phenomenon sans memory, on the other hand, should manifest immediately upon visual

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stimulus presentation Experiments involving manipulation of the time interval between stimulus and response should shed light on the effect's root cause.

So far, inaccuracies in localization have been shown under restricted laboratory conditions in which the subject had to maintain fixation on a single location while viewing a visually impoverished environment containing nothing but a fixation marker. It remains to be seen whether the pattern of localization error will disappear, or generalize in interesting ways if the subject were free to move his/her eyes, or if other objects were present in the environment while the subject maintained gaze on a fixed marker. Unlocking the mechanisms behind the effect could also perhaps elucidate the transition from perception to memory and lead to more direct predictions of neural mechanisms that support it. With these issues in mind, we explored this phenomenon in detail.

1. Materials and methods

All stimuli were presented on a SONY Trinitron monitor (75 Hz refresh; 37.5×28.5 cm) under control of a MAC PowerPC running MATLAB (Mathworks Inc.) and Psychophysics Toolbox (Pelli and Brainard). From a pool of 14 subjects (two authors, 12 naive observers) with normal or corrected-to-normal vision, a subset was chosen for each task. All subjects sat in a normally lit room for experiments described in Figs. 1–3, and in a dark room for experiments in Figs. 4–6. Under room lights, the screen edges were barely visible in the far periphery, and were not seen at all in the dark. Note though, the screen edges are at least 12° from the most peripheral target, hence have little influence on localization judgments. The viewing distance was either 57 or 28.5 cm with the head immobilized by a chin- and head-rest (Handaya Co., Tokyo, Japan). Viewing was binocular.

1.1. Spatial position localization task (LT)

A small circular dot (8 arcmin. diameter) appeared on a computer screen to start each trial. The subject ($n = 10$; eight naive subjects, and two authors) centered his/her gaze on the dot that will, henceforth, be termed the fixation point (FP). After a delay (2 s), a circular target (20 ARCMIN. diameter; in some experiments 40 ARCMIN. diameter targets were used) was briefly displayed for 30 ms at a random location along the horizontal meridian on the screen. The range of target locations was ($0, \pm 25^\circ$) for a viewing distance of 28.5 cm and ($0, \pm 12.5^\circ$) when the viewing distance was 57 cm. The stimulus intensity was at least five times higher than the detection threshold for all subjects. The subject continued to maintain gaze on the FP throughout the

trial. No eye movements were permitted. A fixed time interval (usually 2 s) following target offset, during which the screen was blank except for the small fixation marker, a mouse cursor appeared at the bottom of the screen at a random location within a pre-specified range (denoted by bidirectional arrows in Fig. 1A) of $\pm 3^\circ$ of visual angle from the true target location. Therefore, the distance between the initial location of the mouse cursor and the target location was statistically identical across all possible target positions. The magnitude of movement was thereby controlled for, minimizing the “cursor perception” confound (see Experiment 4 of Musseler, Van der Heijden, Mahmud, Deubel, & Ertsey, 1999). The subject had to drag the mouse and click on the remembered location of the target, while continuing to maintain fixation on the FP. The mouse click terminated the trial. There were 50–60 trials for each subject.

1.2. Relative spatial distance perceptual judgment task (PJT)

A small circular dot appeared in the screen's center at the start of each trial. The subject ($n = 8$; seven naive subjects, one author) fixated on a small, circular dot (FP) to begin each trial, and after a variable delay (750–1500 ms), a pair of circular targets appeared simultaneously (30 ms target on time) along the horizontal meridian at a random pair of spatial locations (spatial range, 0 to $\pm 20^\circ$) on the screen. The targets, one to the left and the other to the right of the FP, were equidistant from it. Following a constant delay after offset of the target pair (inter-stimulus interval, or ISI = 2 s for most experiments, unless stated otherwise), another pair of targets, also horizontally symmetric about the FP, appeared and remained on until the subject responded. The two pairs of targets were displayed in close proximity to one another (maximum separation, 1.5°). The subject then had to report the nearer of the two sequentially displayed pairs to the FP by pressing the appropriate key. The key press concluded the trial. No feedback was provided. There were 100 trials per subject.

2. Results

2.1. Localization errors in pointing responses

First, we investigated the pattern of mislocalizations in motor responses. Subjects had to judge the location of a peripheral target flashed briefly while maintaining fixation on a central dot (FP) displayed on the computer monitor [spatial position localization task (LT)]. Following a constant (2 s) delay after target offset, a mouse cursor appeared at the bottom of the monitor

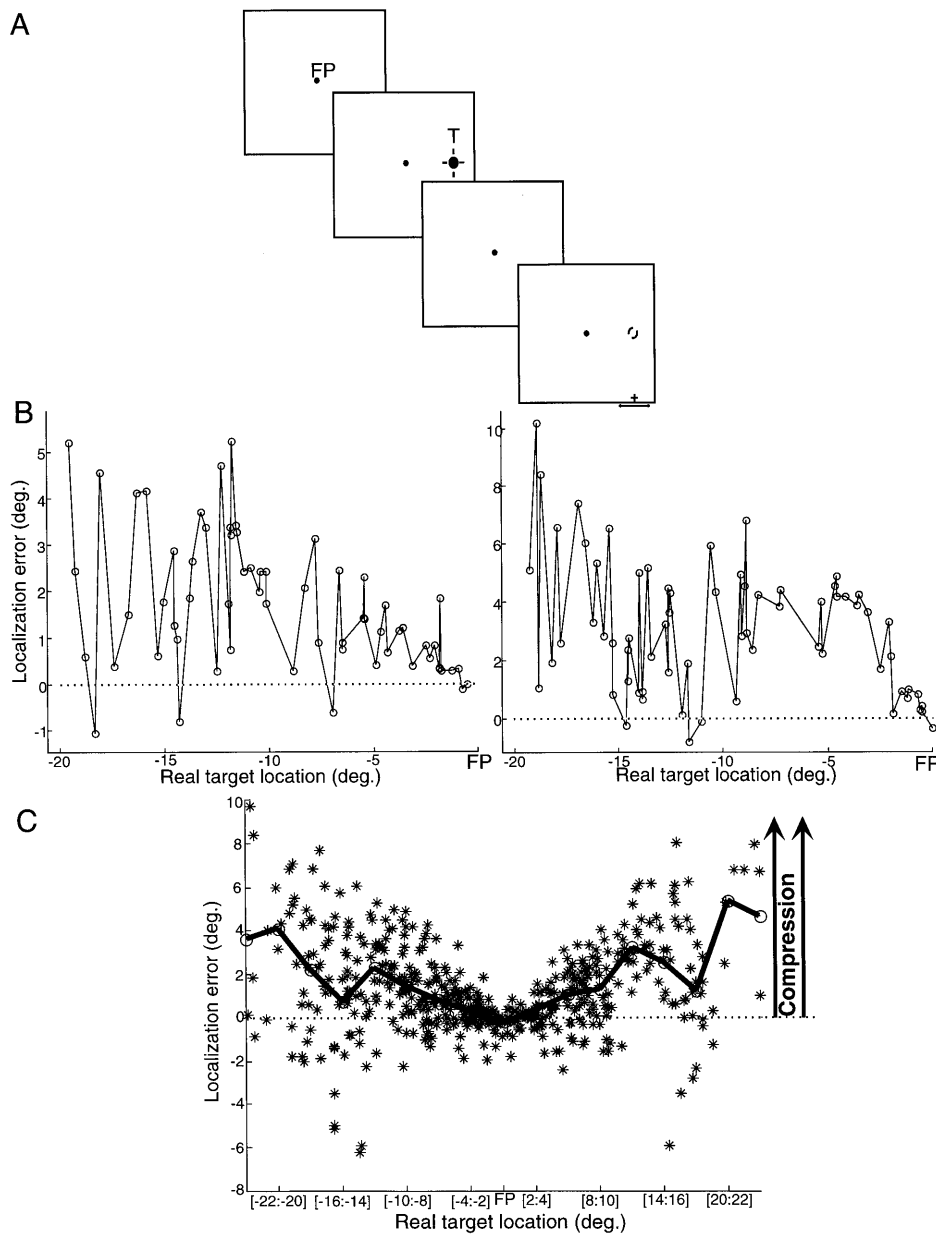


Fig. 1. Undershoot in subjects' pointing estimates of target position. (A) The FP appeared at the beginning of each trial (FP; shown here in the screen's center; some experiments were done with the FP off to one side). After a short delay, a target (labeled 'T') was flashed at a random location along the horizontal meridian. After the target's offset, a mouse cursor (labeled '+') appeared at the bottom of the screen. Its location was chosen randomly from a uniformly distributed, pre-specified range (bidirectional arrows) of distance from the target (the dashed circle is displayed only for the reader's convenience to indicate the location of the already extinguished target). (B) Results from two typical subjects on the LT. Positive values are an underestimate of the target's distance from the FP. The FP was 18° right of screen center (left), and 29° right of center (right). (C) Data from all subjects is shown. Each point represents a single trial. Positive errors indicate foveal displacement. Each point (open circles) along the curve (thick solid line) represents the mean error within the range of target positions specified.

(Fig. 1A). Subjects then had to point the cursor to the remembered target location. Data for two naive subjects are shown in Fig. 1B. The data illustrate the basic finding, namely target position estimates tended to be displaced foveally. Fig. 1C graphs raw data for all ten subjects, and shows both a preponderant undershoot in positional estimates for targets in both left and right visual fields, and the tendency for undershoot magni-

tude to increase with target eccentricity. Error magnitude on a given trial was calculated using the formula.

$$\frac{\text{true target eccentricity} - \text{estimated target eccentricity}}{\text{true target eccentricity}}$$

Positive values indicate a foveal bias. Across subjects, median errors ranged between 0.06 and 0.28 — all positive, demonstrating that all subjects tended to un-

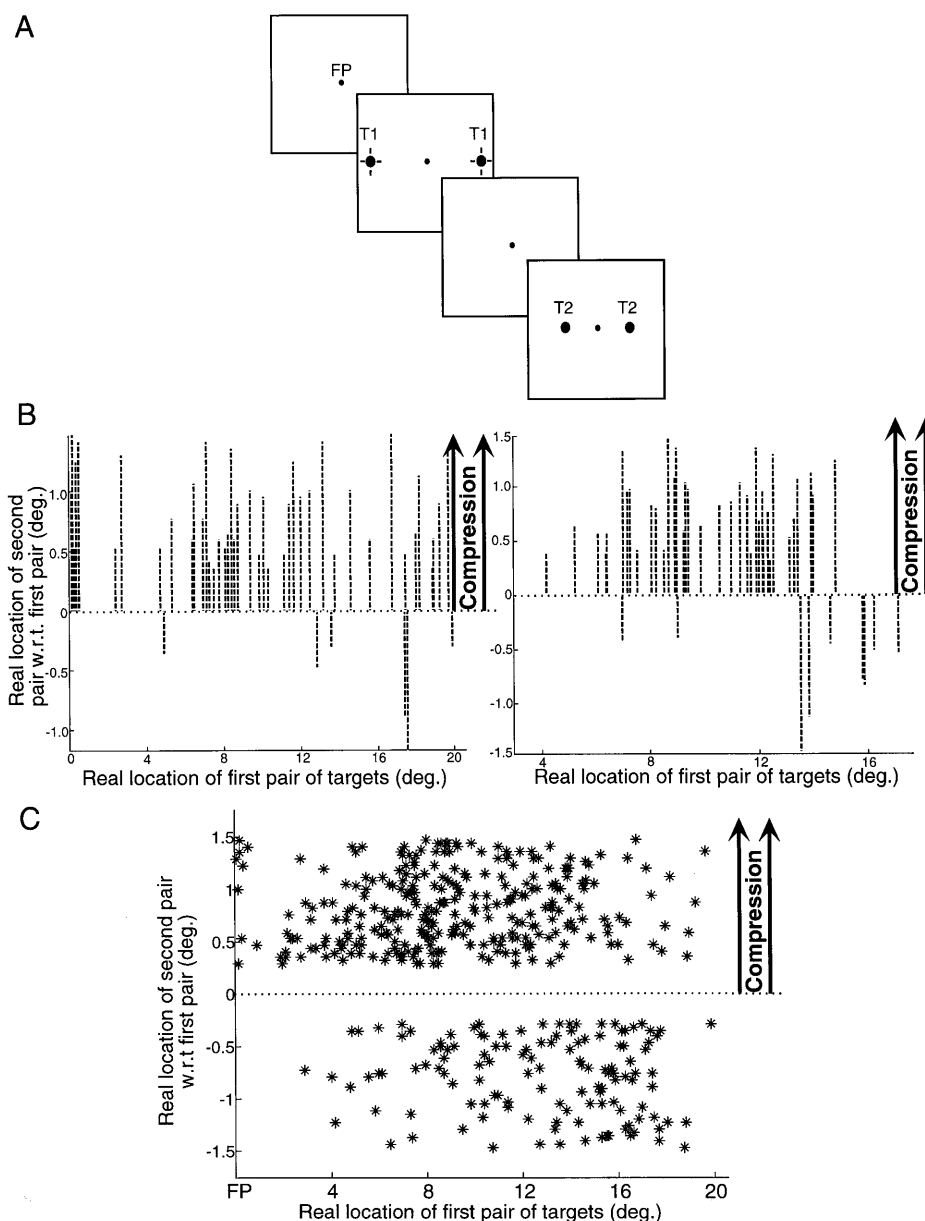


Fig. 2. Systematic errors in perceptual judgments. (A) PJT, The subject fixated on a central FP throughout. A pair of targets ('T1') equidistant from the FP, and on either side of it, were simultaneously flashed. A 2 s ISI following the offset of the first pair, a second pair of targets ('T2'), also horizontally symmetric about the FP, appeared and stayed on until the subject responded. In the figure, the second pair of targets is closer to the FP. (B) Data for two naive subjects on the PJT are shown. Only erroneous trials are shown. Each vertical, dashed line represents a single erroneous trial. Lines above the abscissa represent erroneous trials in which the more recent target pair was actually closer to the FP, and the subject judged incorrectly the first pair to be closer. (C) Data over all subjects are shown. Each point represents a single erroneous trial. Positive and negative values of the ordinate signify the same as in B.

derestimate target eccentricity. Across subjects, the percentage of trials that yielded foveal bias varied between 60 and 97% (mean, 75%; $P < 0.0001$, binomial test).

In a separate experiment ($n = 4$ subjects; one author), we interleaved trials in which the FP was visible and present throughout the trial with trials in which the FP was not visible, even though the subject was still required to maintain gaze on the FP location. As in the visible FP trials, we found a significant compression of visual space on trials in which the FP was not visible

($P < 0.0001$, binomial test). Moreover, the fraction of foveally displaced error trials in the visible versus invisible FP conditions was insignificantly different ($P > 0.6$; binomial test). Hence, the small and inconspicuous FP functioned mainly as a cue for the subject to fixate, and not as a visual landmark. Therefore, compression of visual space occurs independently of whether the FP is visible or not.

The results of a separate task in which subjects ($n = 4$, one author) had to localize targets presented on

the vertical meridian, showed that subjects underestimated significantly vertical target eccentricity as well ($P < 0.0001$, binomial test). Since no eye movements were allowed in any of the tasks described above, and

in principle, the extent of arm movement was the same independent of target location, motor activity per se cannot possibly account for the undershoot.

2.2. Pattern of errors in a task involving perceptual judgments

A possibility remains that while there were no eye movements, planning for one may have given rise to the mislocalization. An alternative possibility is that object location was encoded in terms of its distance relative to some visual landmark (in our case, the FP), and spatial memory for this distance then decayed over time resulting in a memory that stored falsely a code for a shorter distance between the target and the salient landmark. We designed a different task to distinguish between these two hypotheses. In this task, termed the relative spatial distance perceptual judgment task (PJT), a pair of targets, horizontally symmetric about the FP, was presented briefly at random eccentricities. After a constant 2-s delay following the pair's offset, a second pair of targets, identical in stimulus features with the first, was presented. Both targets in each pair were equidistant from the FP, but the relative eccentricities of the two pairs were different. Subjects had to report the pair closer to the FP by pressing the corresponding key. The latter pair stayed on until the subject responded (Fig. 2A). Because both targets in a pair were at the same distance from the FP, and on either side of it, it is difficult to argue for the existence of a plan to execute an eye movement to a single target location. However, since the first target pair was presented in the past compared with the time of response, and that too, for a short time period, the first pair should be pulled closer to the FP relative to the second one. Hence, according to the memory hypothesis, errors, when seen, should be predominantly of the kind where the first, erstwhile target pair is misreported as being closer, even though the second pair is actually closer. Such kind of error is a compressive error. Fig. 2B gives error data from two typical naive subjects. Dashed lines above the horizontal axis represent individual error trials in which the former target pair was misjudged as being closer to the fovea, when it was farther, in reality, than the second pair. Fig. 2B shows that both subjects made, for the most part, compressive errors. Fig. 2C shows error trials pooled across all eight subjects (seven naive observers). A significant majority (69%, range 59–93% across subjects) of lines lie above the dotted line ($P < 0.0001$, binomial test), i.e. the errors were compressive. Over all subjects, the percentage range of incorrect responses was 16–36% (mean, 26%). Compression measures were computed for all erroneous trials separately by using the formula.

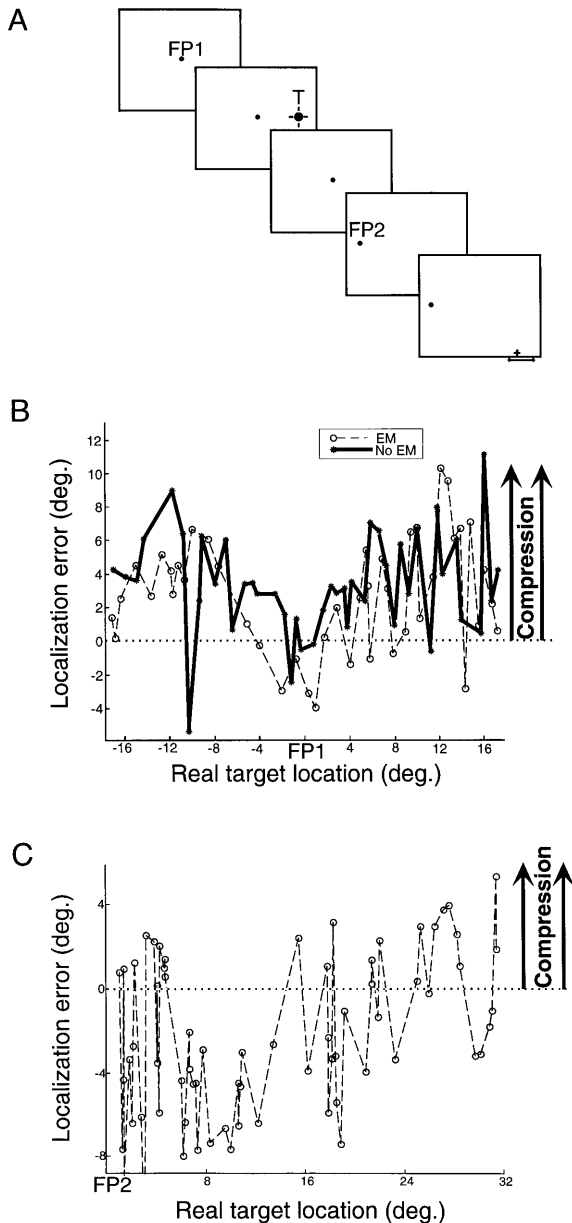


Fig. 3. The role of eye movements in spatial mislocalization. (A) LT with saccadic eye movement(s). A spot (FP) appeared in the screen's center at the start of each trial. Following a time delay, a target (labeled 'T') was flashed briefly in the periphery. After a 500-ms interval, FP1 was turned off, and FP2 (same size, luminance as FP1) was turned on concurrently ($\pm 30^\circ$ eccentricity, randomly chosen on every trial). 1.85 s after target offset, the mouse cursor ('+') appeared. (B) Localization errors with respect to FP1 (center) on both no EM and single EM tasks for one naive subject are shown. Solid lines are no EM trials and dashed lines are single EM trials. Trials in both left and right hemifields are shown. For the purpose of clarity alone, only 20 % of trials are shown. (C) Localization errors with respect to FP2 on the single EM task for the same subject are shown. FP2 is on the left.

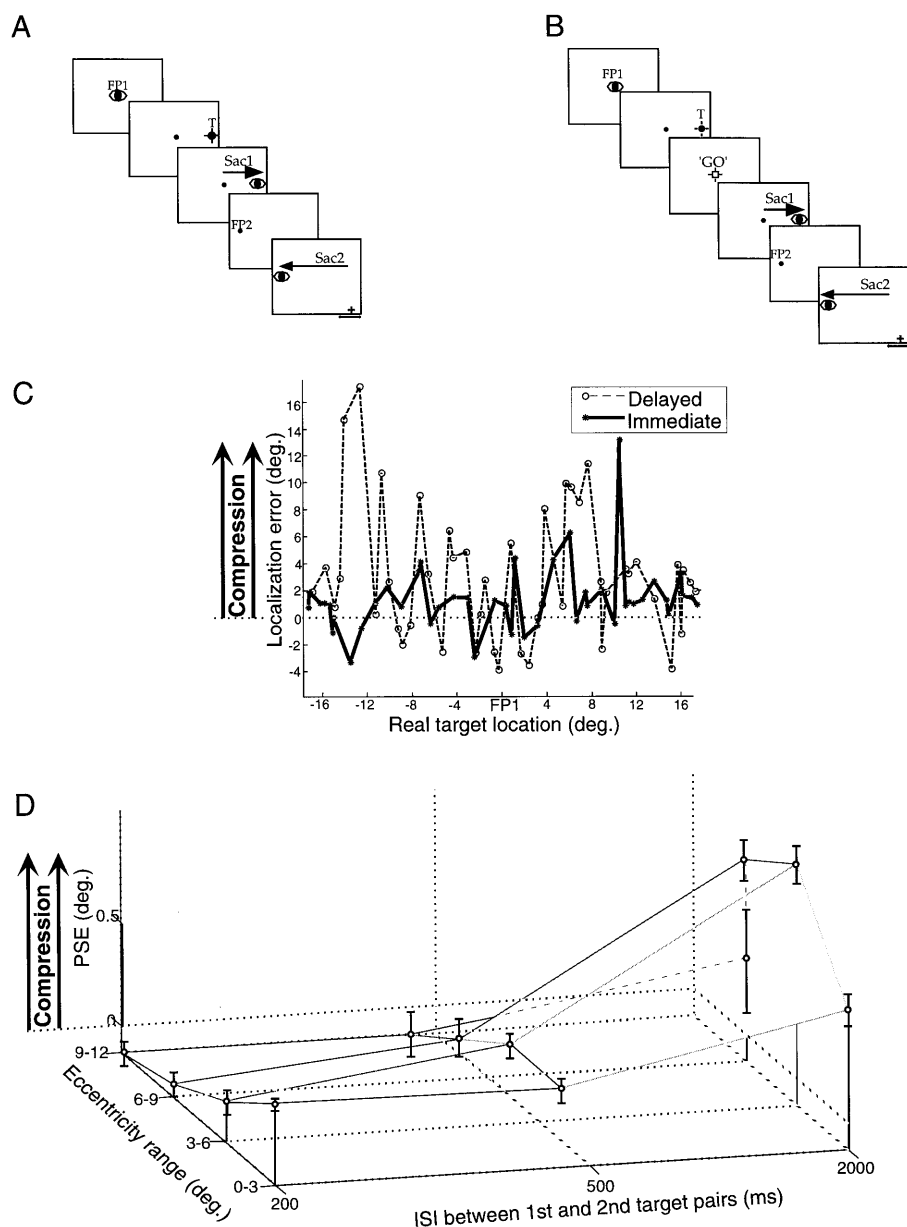


Fig. 4. The effects of time on localization. (A) The sequence of events in the immediate double saccade task. Subject fixates on FP1, target 'T' is then flashed, the subject makes a saccade (Sac1) to the target location, new FP (FP2) is flashed during the saccade, and the subject must then saccade to FP2 (Sac2). (B) The sequence of events in the delayed double saccade task is similar to (A), except that the subject must wait for a signal ('GO') before he/she can move eyes. (C) Localization errors for one subject in the immediate double saccade (solid lines) and delayed double saccade (dashed lines) tasks are shown. For purposes of clarity only, only 20% of trials are shown. (D) Complete spatiotemporal PSE profile of one subject. PSEs obtained from 12 simultaneously conducted randomly interleaved staircase PJTs for four eccentricity ranges (0–3, 3–6, 6–9, 9–12°) and three ISIs (200, 500 ms, 2 s) are shown. Each point is a mean of 15 measurements. Error bars represent ± 1 S.E.M. A positive PSE is obtained if the first pair must actually be more peripheral in order for both pairs to be subjectively perceived as being at the same eccentricity.

$$\frac{\text{former target pair eccentricity} - \text{latter target pair eccentricity}}{\text{former target pair eccentricity}}$$

Compressive errors were positive, expansive were negative. Across subjects, median compression measures ranged between 0.05 and 0.15 — all positive.

Thus, results from the perceptual judgment task corroborate the hypothesis that mechanisms underlying

perception or visual, spatial memory, and not motor activity or motor planning, form the basis for the effect.

2.3. Localization errors and eye movements

We have provided evidence for a foveally biased pattern of mislocalization errors. Does this pattern manifest only under limited viewing conditions in which

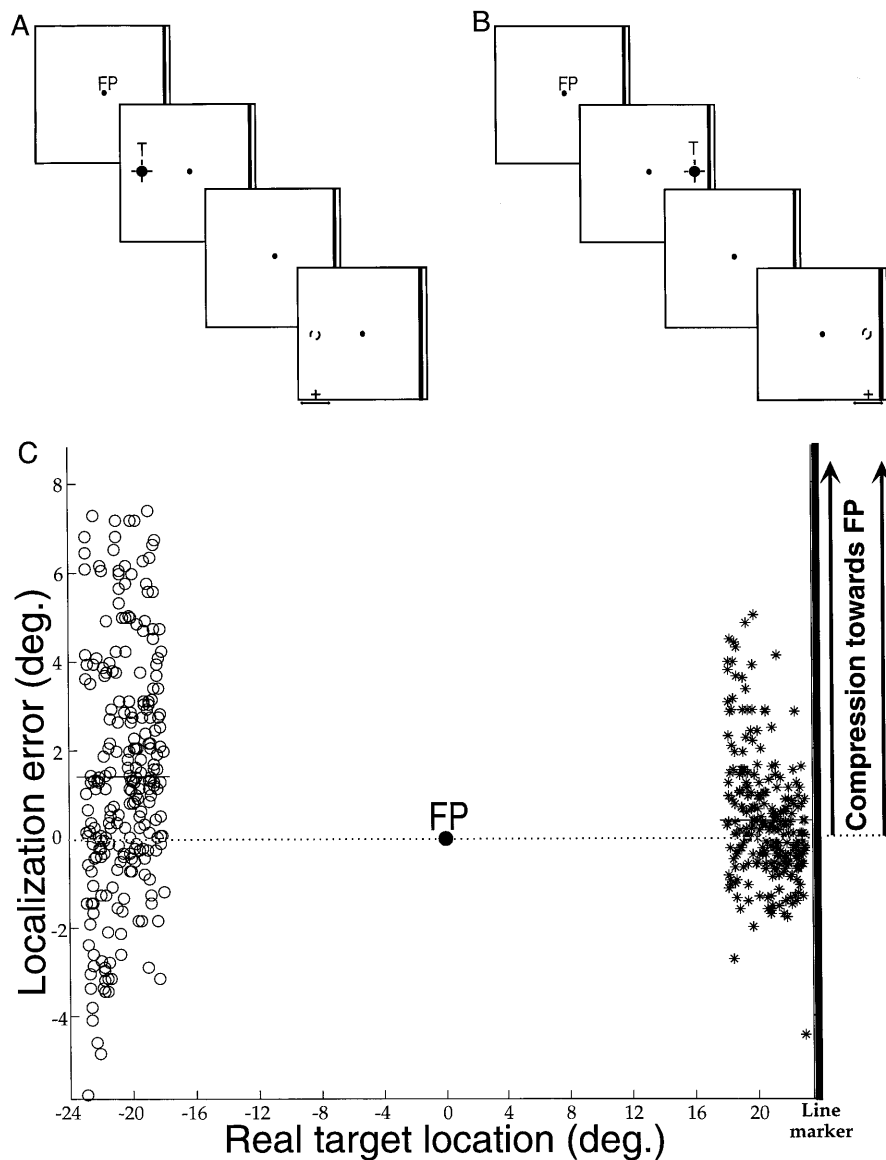


Fig. 5. Localization in the presence of a permanent, visually salient reference. (A and B). The timeline of the task is shown. The subject had to fixate on a central FP. A vertical line (10 arcmin in width) spanning the height of the monitor was presented 24° on the right, and stayed on throughout. In randomly interleaved trials, a target (labeled 'T') appeared either in the left (A), or right (B) hemifield. The target location was within a pre-specified range of eccentricities ($\pm 18^\circ$, $\pm 23^\circ$). (C) Data from all five subjects are plotted. Trials in which the target appeared in the left hemifield are represented as open circles, shown on the left; targets presented in the right hemifield are indicated as asterisks, and are on the right. Each point (circle or asterisk) denotes a single trial. The dashed line is the horizontal meridian. Mean localization errors for each of the two populations of targets near to (mean error = 0.4°), and distant from (mean error = 1.4°) the line marker are shown as horizontal solid lines.

subjects cannot make eye movements? Relatedly, if the FPs during target presentation and later during observer action are not the same, will the estimates be biased towards the original FP while the target is displayed, and thus argue for coding of target position in exocentric coordinates, or towards the new FP the subject has to fixate on while responding, thus arguing for an egocentric (eye-centered) coordinate system? To address these issues, we devised a variant of the LT (single-EM task; Fig. 3A). As before, the subject fixated on a central FP1, and then a target (T) was momentarily turned on as before. 500 ms after target offset, FP1

was turned off and a new FP2 concurrently turned on. FP2 was located at a constant horizontal eccentricity (30°), but was located randomly either in the left or right visual field on a given trial. The subject had to saccade to FP2 as soon as possible, and then maintain gaze during pointing. Localization errors obtained in this condition were compared with a control (no-EM task) in which the subject fixated on FP1 throughout under an identical stimulus sequence. As can be seen from the overlap of the two curves in Fig. 3B, there is no gross difference in the pattern of error between the two tasks. So, eye movement, and re-fixation did not

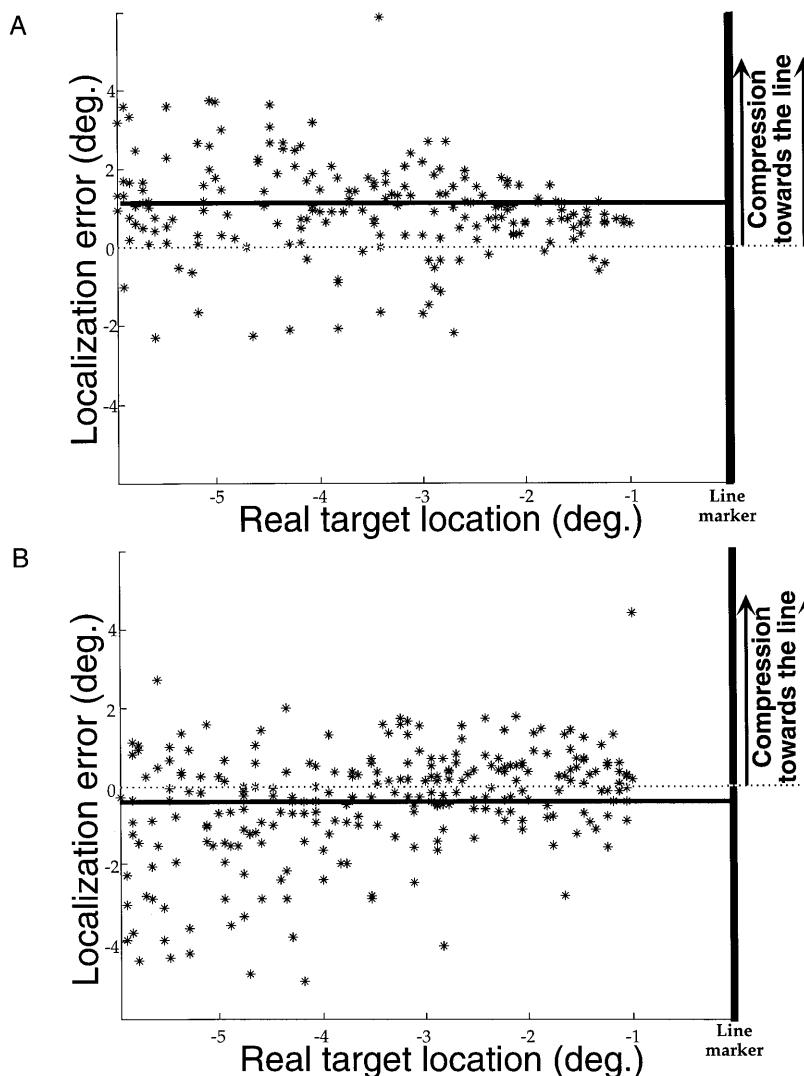


Fig. 6. The pattern of localization errors with respect to the line. (A) Only trials in which the target appeared near the line are shown. The line is shown on the extreme right (0°). All targets (asterisks) were presented to the left of the line. The mean error (1.1°) is represented by a solid horizontal line in the figure. Most points lie above the dotted line indicating positive error. (B) For comparison, localization errors with respect to the line marker in the previous task (FP in center) are shown. Only trials in which the target appeared near the line marker are shown. The mean error (solid line) was -0.4° .

abolish the bias towards the initial FP (FP1), although the amount of error was reduced marginally. Since the target was not flashed immediately before (≤ 50 ms) or during the saccade as was the case in eye movement experiments (Matin, 1972; Honda, 1993; Honda, 1995; Cai et al., 1997; Ross et al., 1997), but at least 500 ms before, we did not find a similar compression of visual space centered on the saccade goal, FP2 (Fig. 3C). Lappe, Awater, and Kregelberg (2000) have shown that presaccadic compression centered on the saccade goal is negligible for targets presented ≥ 100 ms before saccade onset, consistent with our present findings. Thus, our results argue strongly for target position being stored in exocentric, not egocentric coordinates. Finally, our effect was found to be relatively insusceptible

to subsequent eye movements, confirming the effect's robustness and generality.

2.4. Relationship between time and the nature of the error

Next, we explored other possible causes for the mislocalization. Data (not shown) from a slightly modified PJT with a very short 30 ms ISI did not show a systematic pattern in localization error (two subjects). These results are not too surprising, since the experiment is similar to past, simultaneous vernier acuity experiments (Westheimer & MccKee, 1977). More pertinently, these preliminary findings suggested to us that time delays could be vital to explaining the effect.

To investigate systematically the role of time, two variants of the LT were designed. In the first variant (immediate double saccade task; Fig. 4A), the subject had to make two saccades — the first from FP1 to the target as soon as the target first appeared, and immediately after, a second from the target to the new FP (FP2) in the periphery. In the second variant (delayed double saccade task; Fig. 4B), the subject still had to make the same two saccades, but had to wait 2 s after target offset for a change in FP1 color before the first saccade could be initiated from FP1. Data for one subject, shown in Fig. 4C, clearly show both more numerous compressive errors, and a larger magnitude of compression in the delayed double saccade task (dashed line) compared with the immediate double saccade one (solid line). All three subjects tested showed an identical pattern of results — a mandatory 2-s time delay in the double saccade task significantly enhanced the degree of displacement towards FP1 (Wilcoxon rank sum test, comparing data from the two tasks for each subject individually, $P < 0.05$). Thus, consistent with a memory-based explanation for the effect, time delay between stimulus presentation and response seems critical in the development of a systematic bias in estimates of target position.

To further elucidate the consequences of time delay, we had six subjects participate in a PJT with three randomly interleaved ISIs: 200, 500 ms, and 2 s. The distance between the two pairs was changed for the corresponding eccentricity range and ISI after each trial in 0.3° steps according to the method of limits (Guilford, 1954). Based on the previous results, we anticipated that with increasing ISI, the pair presented first would be foveally displaced by increasing amounts. For both 500 ms and 2 s ISIs, the first pair had to be physically more peripheral in order for both pairs to be perceived subjectively as being at equal eccentricity. This difference in eccentricity, also called the point of subjective equality (PSE), is shown in Fig. 4D for one subject over a range of eccentricities (0 to $\pm 12^\circ$) and for all three ISIs. The graph shows that the mislocalization (positive values of the PSE indicate compression in perceived eccentricity of the first pair relative to the second) appeared to increase with ISI, as predicted. All subjects yielded greater PSE values on the 500 ms and 2 s ISI PJTs compared with the 200 ms ISI one; five of six subjects showed more positive PSEs on the 2 s ISI PJT as compared with the 500 ms ISI one. Thus, the amplitude of compression enhances with time, a telltale symptom of a memory phenomenon, as opposed to a purely perceptual one.

Owing to the strong dependence of bias on time, it is natural to implicate processes underlying memory decay. A second memory-based hypothesis is also tenable. Since compressive localization errors were fewer and smaller in magnitude (although not completely absent) in the 200 ms ISI PJT as compared with the 500 ms and 2 s ISI PJTs, it is conceivable that a re-encoding of target position took

place in the conversion from an accurate, but short-lived iconic store (Sperling, 1960) to a less accurate, but longer lasting short-term or working memory store (Baddeley, 1986). Note that subjects typically took more than a second to respond after the second pair came on even on the 200 ms ISI PJT. So the time between the offset of the first target pair and response was considerably longer than the maximum half second duration of iconic memory. Moreover, iconic memory has been shown to be encoded in purely retinal coordinates (Averbach & Sperling, 1960). Fig. 3B however, proves that unlike a retinal code, localization judgments do not change in step with eye position, but are instead firmly anchored to the original eye position at the time of target presentation. In a separate experiment, we found that varying the viewing distance did not change the mean error in absolute screen coordinates, showing that target position was not encoded in retinocentric coordinates, but in an external, environmental coordinate system. Based on these observations, memory re-encoding seems unlikely. A simpler hypothesis of a spatial, working memory system that gradually gets increasingly biased in time appears more likely to be true.

Having ascertained that the length of the time *interval* between presentations was critical, we wondered whether the time *duration* of target presentation mattered at all (Schlag & Schlag-Rey, 1995). Presumably, a longer duration of the target should render positional estimates more accurate. Nonetheless, if the ISI remains the same, direction of bias in the error should also remain unchanged i.e., the first pair of targets should be incorrectly judged as being closer to the FP than the second pair more often than vice versa. To verify our prediction, we tested five subjects on three variants of the PJT, with an identical 2 s ISI between the two pairs. The first task was as before; the first pair was presented transiently while the second stayed on until the subject's response. The second variant reversed the durations of the two pairs — the pair presented first remained on for 4 s (sustained), while the second pair was now presented briefly (30 ms). In the third task, both pairs were flashed. As expected, subjects made the fewest errors in the second task, and the most in the third [percent erroneous trials (means across the five subjects), 27, 16, 35%, respectively]. More importantly, the pattern of errors was the same, the first target pair, irrespective of whether it was transient or sustained, was misjudged more frequently to be closer to the FP on trials in which the second pair actually was. Respectively, across condition, 72, 73 and 62% of all errors were of this type. For each, the difference between the two types of errors was significant (Wilcoxon rank sum test, $P < 0.0001$ for each). Since the ISI on all three conditions was identical (2 s), the bias was maintained. Therefore, these findings too confirm that time between stimulus offset and response — the time in spatial memory — is critical in explaining the bias. To summa-

rise, we have shown that memory for the spatial position of a stimulus has a directional bias in favor of a stable frame of reference (so far, the FP only), and this bias gets progressively enhanced with the passage of time following target offset.

2.5. Localization errors in the presence of an unfixated, visual landmark

In our everyday experience, we encounter visually rich environments with many salient objects in them that are capable of grabbing our attention. Does the presence of a visually salient object on the screen affect localization? It is conceivable that, with the addition of a second, stable frame of reference, estimates of target location become more accurate, but how would the relative proportions of undershoot to overshoot in localization error be affected? It is possible for the direction of bias to remain the same, while independent of error direction, the error magnitude could concomitantly decrease. On the other hand, all stable frames of reference may share the property that memory of object locations is pulled towards them. If this were the case, on trials in which the FP and the visual landmark happen to lie on opposite sides of the target, the degree of foveal displacement should decrease. Thus, according to the first hypothesis, fixation is unique and estimates of target position are biased exclusively towards the center of gaze, whereas according to the second hypothesis, estimates of target location can be displaced by other non-fixated references in addition to fixation. To resolve this question, we had subjects do another localization task in which the stimulus display was modified slightly from the one used in LT (see Fig. 1). In the new task, a vertical line appeared in the right visual field in addition to a central FP (Fig. 5A and B). Both line and FP remained visible throughout the trial. On a given trial, either the FP and line were both to the right of the target (Fig. 5A; baseline) or were located on opposite sides of it (Fig. 5B) 2 s after target offset, the cursor became visible and the subject placed the cursor where he/she remembered perceiving the target location. Fig. 5C shows the data for all subjects ($n = 6$). Each point represents a single trial and positive values of error indicate foveal displacement. As expected, for targets located in the right hemifield (Fig. 5B), accuracy of position estimates improved, and foveal bias, although still present, was reduced significantly compared with baseline (Fig. 5A). Positional estimates of 69% of targets presented in the left visual field were displaced foveally, compared with a significantly smaller 56% for targets shown in the right visual field and closer to the line (Wilcoxon rank sum test, $P < 0.005$). So, positional estimates were not displaced as strongly towards the FP as before when the visual landmark was located nearby. In accordance with the second hypothesis above, the

center of gaze is not singular; it is but one example of a frame of reference — others defined by visual salience — that can alter estimates of target location.

Unlike experiments described so far, in which subjects had to fixate on a point in space for several seconds, we are free to move our eyes around in daily life. In the absence of a point in space to fixate on, the question remains whether non-fixated, stable visual references could introduce a directional bias in localizing targets. In a new task conducted to examine this question, the subject was allowed to move freely his/her eyes while a display containing a bright vertical line in the far right periphery was presented. Subjects were instructed explicitly not to look directly at this otherwise highly visible landmark, but instead, to ignore it. From the previous experiment, we predict that since the line provided the only reference, estimates of target positions should be systematically biased towards it. As expected, a displacement in estimates of target position towards the vertical line was seen. Fig. 6A shows the data across all subjects ($n = 4$, two authors, two trained psychophysicists naive to the task) for targets actually located left of the line. On 68% of such trials, estimates of target position were displaced significantly towards the line (binomial test, $P < 0.0001$); in comparison, only 14% of targets located left of center, and far from the line were localized towards it. Hence, in the condition in which subjects were free to move their eyes, estimates of the locations of briefly presented targets were displaced towards temporally unvarying, conspicuous objects in the environment. Combining the data shown in Figs. 5 and 6A, we conclude that memory of target location is distorted by the presence of temporally rigid frames of reference. Examples of such reference frames include the center of gaze, and visually salient landmarks.

We re-plotted the data with respect to the line from trials of the previous experiment in which gaze had to be maintained on the FP. For trials in which the FP and line were on opposite sides of the target (Fig. 6B), there was no such displacement towards the line. Estimates of target location were no more likely to be biased closer to the line. In fact, the mean error in the previous task (Fig. 6B; solid line) was negative (-0.4°), and there was a small but significant bias away from the line (towards the FP; $0.01 < P < 0.05$, Wilcoxon rank sum test). It is possible that different reference frames exert variable degrees of pull; perhaps the center of gaze is more powerful in this respect than a landmark.

3. Discussion

We have shown that there is a systematic tendency to mislocalize targets towards a stable frame of reference.

Our experiments eliminated the possibility that there is an inherent bias in the motor program subserving movement (Figs. 1 and 2). Contrary to our findings, others (Bock, 1986, 1993) have found an overshoot in localization judgments. However, there are at least two fundamental differences in the experimental design. In Bock's experiments, subjects had to localize a target that remained present throughout. Second, the hand was hidden from the view of the observer during the entire time period that the arm moved. In our work in contrast, the target must be extinguished at least before movement completion in order to get an effect, and the mouse cursor was always visible to the observer. We believe that the lack of visual feedback is key in explaining the overshoot, and Bock's effect may be one of motor control, not sensation or sensory memory. It has been shown that the amplitude of voluntary saccadic eye movements is systematically smaller than the real distance to the goal (Weber & Daroff, 1972; Prablac & Jeannerod, 1975). Thus, foveal bias is general across effectors (eye and arm), and, as we showed above (Fig. 2), is also found when only perceptual judgments are required. Therefore, motor circuitry or motor planning cannot be the cause of our effect. It may be, however, that a general-purpose system that provides the metric in perceived visual space is also in charge of guidance of eye movements (Musseler et al., 1999). Irrespective of whether or not eye movements need to be made to a stimulus, its positions will be encoded automatically in memory. Some of the stimuli may become future goals for eye movements, some others may turn out to be stimuli to avoid. In either case, the stored positions will be useful.

Misperceptions of target position at the time of its presentation, or soon after, cannot be the reason either. If the bias were perceptual, it should peak while the target was present or immediately after its offset. However, the bias was shown to increase over time following the offset of the target (the double saccade experiment and PJT, Fig. 4). Instead, we propose that spatial, working memory is systematically distorted by the presence of references. The locations of objects presented earlier are *remembered* falsely as being closer to salient reference frames than they really are. Memories of the positions of evanescent targets are thus biased in competing directions by different frames. In a real world replete with myriad salient objects, this tug-of-war could lead ultimately to a more accurate memory of spatial location.

In the present study, landmark saliency was empirically ascertained: displacement in positional estimates towards a landmark rendered the landmark salient. By this criterion, the FP is a salient landmark. As shown above, in the experiment involving visible and invisible

FP markers, FP visibility was not necessary for salience. Other factors such as attention must also be considered as playing a part, since the focus of attention is usually coincident with the center of gaze. Similarly, the visually conspicuous line (Figs. 5 and 6) is also a salient landmark by our working definition. Future work will determine whether visual landmarks defined by shape, texture, color or other salient pop-out features, landmarks defined by proprioceptive cues, and landmarks defined in other sensory modalities are similarly salient. For a landmark to be effective in biasing positional estimates towards it, we believe it should be present perhaps during, and certainly immediately following target presentation (Lappe et al., 2000). In our eye movement experiment (Fig. 3), estimates of target position were displaced towards FP1 — the FP at the time of target presentation, and 500 ms subsequent to target offset — while no such displacement towards FP2: the ensuing FP that subjects fixated on while pointing: was seen. Put another way, our eye-movement experiments indicate that spatial, working memory is anchored to the reference frame at the time of memory consolidation just following target offset, and not to the reference frame at the time of retrieval. This is in stark contrast to retrieval cue-dependence memories found with semantic and episodic memories (Tulving, 1972), wherein the cue at the time of memory recall distorts performance. We conjecture that the low-level, sensory, pre-cognitive nature of the memory tested here may be a differentiating factor. In separate PSE perceptual judgement experiments (data not shown), foveal bias in estimates of target distances relative to a salient frame of reference was found to reach a maximum for an ISI of 3 s between the two target pairs ($n = 4$; staircase tasks of 2, 3, 6 and 10 s ISIs were randomly interleaved). A time period of a few seconds may be the amount of time that spatial, working memory remains unstable and susceptible to external biases.

Musseler et al. (1999) also have elegantly shown that the amplitude of mislocations increases with retinal eccentricity. In their relative judgement task, the mid-position of a spatially extended, briefly flashed comparison stimulus was foveally displaced compared to the position of a flashed probe. When the probe followed the comparison stimulus with increasing stimulus onset asynchrony, or SOA, the size of the mislocation increased, consistent with our findings. However, even when the probe appeared before the comparison stimulus (SOA = 112 ms), the effect, namely foveal displacement of the comparison stimulus, persisted to the same degree, in variance with our findings. The contradictory results between the two studies may be owing to the different stimuli used. In their study, the comparison stimulus was longer, and extended farther into the

periphery than the probe¹. In fact, Musseler et al. found that when the probe and comparison stimulus were the same size, the effect went away, compatible with a temporal explanation. Their apparently contradictory findings are indeed consistent with a memory-based explanation. Our studies are different in several other important ways. In our hands, the effect is more robust and long lasting. Mislocalizations can be of the order of several degrees of visual angle, and the effect peaks 3 s following stimulus presentation; it asymptotes at 300 ms for Musseler et al. This is critical since a 2–3-s time period is too long for eye movement tendencies to endure, a possibility Musseler et al. suggest. Moreover, we show that the mislocalization is independent of eye movements (Fig. 3). In addition, we show that fixation is but one example of a frame of reference that can distort visual space. Visual salience can also provide an effective biasing force (Fig. 6).

We are now left with the question, why does compression increase with distance from the reference? Assuming coding of stimulus position with respect to distance from the landmark, with increasing distance from the reference, increased noise in localization judgments is likely. Enhancement in jitter as a monotonic function of distance modulated by a tendency to compress visual space leads naturally to a greater magnitude of compression with greater distance.

Future experiments will shed light on the neuroecological utility of this phenomenon. One possibility is based on the assumption that accurately storing spatial locations of objects in an analog code in the brain is demanding. Hence, remembering locations of targets in space in relation to a salient frame of reference is both more meaningful and neurally economical (Anderson & Schooler, 1991). Compactness in the code for the landmark-based coordinates of objects, and in the process, consequent compression in object distance relative to the landmark reference, perhaps allows the organism to have both more unused storage space and more efficiently organized spatial knowledge about the environment, thereby freeing resources to tackle the uncertain future.

¹ The peripheral edge of the comparison stimulus will be foveally displaced by a greater amount as compared to the central edge (Fig. 1). Therefore, even when the probe appears a very brief time before the comparison stimulus (–112 ms SOA), this inhomogeneous compression would cause the mid-point to be foveally displaced more than the probe. Compression increases with time and space (eccentricity), and their design confounds the two variables. Moreover, estimating the mid-point of a stimulus is somewhat demanding, and processing of the comparison stimulus may therefore pre-empt processing of a probe presented moments ago, and be stored first in memory. Naturally, computing the mid-point takes but finite time. So, our memory-based explanation would predict that for a sufficiently long SOA (400 ms, say), the mislocalization will be greater when the comparison stimulus is presented first, compared to the reverse condition in which the probe is presented first.

What is the neurophysiological basis for the mislocalization? One possibility is based on lateral connections connecting cells in a given cortical area. It is reasonable to assume that the landmark and the briefly presented target will cause two non-overlapping groups of cells to fire at the beginning of the trial — one corresponding to the landmark, and the second to the target's location in space. Cells whose RFs lie between the target and landmark will be activated by horizontal connections. Once the target is turned off, the activity of cells for whom the target lies in their RFs will die down gradually over the delay period (Mazzoni, Bracewell, Barash, & Andersen, 1996; Chafee & Goldman-Rakic, 1998). Since the neighboring cells receive recurrent activity from both the landmark and the target, their activity will build up during this time period. As a result, the peak of activity corresponding to the target will shift in time to lie closer to the landmark.

Alternatively, one can posit the existence of probability summation cells downstream that pool activity from lower-level cells with neighboring RFs. Sustained activity corresponding to a stable frame of reference and decayed, relatively lower activity corresponding to the target presented earlier are summed by such cells, bias assessment of the target's position to be closer to the reference frame. Of course, these are two among several possible candidates for explaining the bias. We believe that the prefrontal cortex, which has been implicated in spatial memory (O'Keefe, Wilson, & Goldman-Rakic, 1999; Rao, Williams, & Goldman-Rakic, 1999), and the hippocampal formation, known for place cells that fire in relation to distance from a stable landmark (Bohbot et al., 1998; O'Keefe, Burgess, Donnett, Jeffery, & Maguire, 1998), may be promising neural sites for investigation.

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References

- Anderson, J. R., & Schooler, L. J. (1991). Reflections of the environment in memory. *Psychological Science*, 2, 396–408.
- Averbach, E., & Sperling, G. (1960). Short-term storage of information in vision. In C. Cherry, *Fourth symposium on information theory*. London: Butterworths.
- Baddeley, A. (1986). *Working memory*. Oxford: Clarendon.
- Bock, O. (1986). Contribution of retinal versus extraretinal signals towards visual localization I goal-directed movements. *Experimental Brain Research*, 64, 476–482.
- Bock, O. (1993). Localization of objects in the peripheral visual field. *Behavioural Brain Research*, 56, 77–84.

- Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, 36, 1217–1238.
- Cai, R. H., Pouget, A., Schlag-Rey, M., & Schlag, J. (1997). Perceived geometrical relationships affected by eye-movement signals. *Nature*, 386, 601–604.
- Chafee, M. V., & Goldman-Rakic, P. S. (1998). Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task. *Journal of Neurophysiology*, 79, 2919–2940.
- Guilford, J. P. (1954). *Psychometric methods*. New York: McGraw-Hill.
- Helmholtz, H. V. (1866). *Handbuch der physiologischen optik*. Leipzig: Voss.
- Honda, H. (1993). Saccade-contingent displacement of the apparent position of visual stimuli flashed on a dimly illuminated structured background. *Vision Research*, 33, 709–716.
- Honda, H. (1995). Visual mislocalization produced by a rapid image displacement on the retina: examination by means of dichoptic presentation of a target and its background. *Vision Research*, 35, 3021–3028.
- Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature*, 403, 892–895.
- Mateeff, S., & Gourevich, A. (1983). Peripheral vision and perceived visual direction. *Biological Cybern.*, 49, 111–118.
- Matin, L., Jameson, D., & Hurvich, L. (1972). *Handbook of sensory physiology*, vol. 7/4 (pp. 307–332). Berlin: Springer.
- Mazzoni, P., Bracewell, R. M., Barash, S., & Andersen, R. A. (1996). Motor intention activity in the macaque's lateral intraparietal area. 1. Dissociation of motor plan from sensory memory. *Journal of Neurophysiology*, 76, 1439–1456.
- Mewhart, D. J. K., & Campbell, A. K. (1978). Processing spatial information and the selective masking effect. *Perception of Psychophysics*, 24, 93–101.
- Mitrani, L., & Dimitrov, G. (1982). Retinal and visual localization during pursuit eye movements. *Vision Research*, 22, 1047–1051.
- Musseler, J., Van der Heijden, A. H. C., Mahmud, S. H., Deubel, H., & Ertsey, S. (1999). Relative mislocalization of briefly presented stimuli in the retinal periphery. *Perceptions of Psychophysics*, 61, 1646–1661.
- O'Keefe, J., Burgess, N., Donnett, J. G., Jeffery, K. J., & Maguire, E. A. (1998). Place cells, navigational accuracy, and the human hippocampus. *Proceedings of Royal Society of London-B. Biological Sciences*, 353, 1333–1340.
- Osaka, N. (1977). Effect of refraction on peripheral locus of a target in peripheral visual field. *Journal of Psychology*, 95, 59–62.
- O Scalaidhe, S. P., Wilson, F. A. W., & Goldman-Rakic, P. S. (1999). Face-selective neurons during passive viewing and working memory performance of Rhesus monkey: evidence for intrinsic specialization of neuronal coding. *Cerebral Cortex*, 9, 459–475.
- Prabla, C., & Jeannerod, M. (1975). Corrective saccades: dependence on retinal reafferent signals. *Vision Research*, 15, 465–469.
- Rao, S. G., Williams, G. V., & Goldman-Rakic, P. S. (1999). Isodirectional tuning of adjacent interneurons and pyramidal cells during working memory: evidence for microcolumnar organization in PFC. *Journal of Neurophysiology*, 81, 1903–1916.
- Rauk, M., & Luuk, A. (1978). Perceived visual direction of the brief test-flashes on the horizontal scale. *Acta Comment. Universitatis Tartuensis*, 474, 900–1000.
- Ross, R., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature*, 386, 598–601.
- Schlag, J., & Schlag-Rey, M. (1995). Illusory localization of stimuli flashed in the dark before saccades. *Vision Research*, 35, 2347–2357.
- Seal, J., & Commenges, D. (1985). A quantitative analysis of stimulus-related and movement-related responses in the posterior parietal cortex of the monkey. *Experimental Brain Research*, 58, 144–153.
- Sneider, B., & Ehrlich, D. J. (1978). Changes in the apparent lengths of lines as a function of degrees of retinal eccentricity. *Perception*, 7, 215–223.
- Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, 386, 167–170.
- Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs*, 74, 29.
- Townsend, V. M. (1973). Loss of spatial and identity information following a tachistoscopic exposure. *Journal of Experimental Psychology*, 98, 113–118.
- Tulving, E. (1972). Episodic and semantic memory. In E. Tulving, & W. Donaldson, *Organization of memory*. New York: Academic Press.
- Westheimer, G., & MccKee, S. P. (1977). Spatial configurations for visual hyperacuity. *Vision Research*, 17, 941–947.